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Chapter 6

Domestication and Welfare in Farmed Fish

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Abstract

The domestication of fish species is still in its early stages when compared to terrestrial animals. The effects of domestication on welfare of farmed fishes are complex to study because fish differ from livestock in genetics, physiology and behaviour, and experience different sensory worlds. Consequently, empathy with fish and understanding of their needs becomes more problematic than with land animals. Additionally, the acknowledgement and study of mental dimensions of fish existence is very recent. We discuss that higher levels of domestication in fish do not necessarily correspond to better welfare because (1) artificial selection by the aquaculture industry is mostly focused on production-related traits such as growth, and this selection process may have unknown negative effects on welfare-related traits; (2) the number of fish species presently farmed (*circa* 300) is 10-fold higher than land animals, rendering the establishment of standard welfare guidelines extremely complicated; (3) the current paradigm of the Five Freedoms guiding welfare is out-dated and was designed for livestock; and (4) there are still severe knowledge gaps in the biology of farmed fishes, especially in welfare-related traits. The implementation of humane farming systems should integrate industry, science and ethics in an open dialogue in order to produce relevant results.

Keywords: artificial selection, fish, behaviour, aquaculture, welfare

1. Introduction

1.1. Domestication

Domestication is a human-induced process that gradually changes a cultured organism. It extends over generations and involves developmental effects within each generation, culminating

generally in genetic changes across generations [1]. One of the first domesticated animals was the goat (*Capra hircus*), in a process that started over 10,000 years ago in Iran [2]. Present-day domesticated goats are therefore the product of a long-lasting human selection of animals and breeders carrying specific traits in meat, fur, milk and docile behaviours, and also natural selection for fitness under variable conditions [3]. To put things in perspective, fish domestication is a much more recent process: while exceptions such as carp (*Cyprinus carpio*), tilapia (*Oreochromis niloticus*) and goldfish (*Carassius auratus*) may have possibly been artificially selected for hundreds of years, and another 12 species such as cod (*Gadus morhua*), salmon (*Salmo salar*) and trout (*Oncorhynchus mykiss*) in the 1800s [4], the vast majority of farmed fish has been under domestication merely since the middle of the twentieth century [5–8].

Although the usual interpretation of animal domestication has been related to genetic changes induced by artificial selection [9], developmental effects have been gathering more interest recently due to the increasing number of domesticated species and purposes of captive breeding [1]. These developmental responses are especially important in fishes because they present remarkably high levels of phenotypic plasticity, much more than terrestrial vertebrates [10, 11]. In Sections 2.1 and 3.1 of the current text, we will dive deeper into these matters. But in fact, this plasticity allows fish to adapt their phenotype to rearing conditions, which, taking into account their recent domestication process, makes fish domestication a controversial issue: although there is variation in morphology, physiology and genetics between farmed fish species and their wild conspecifics [12–14], it is generally much lower than between terrestrial farm animals and their wild counterparts [4, 9, 11, 12]. Nevertheless, it is mostly established that fish farmed under well-managed systems (i.e. that provide conditions that enhance growth and survival while supplying the correct nutrition regimes for the species) can maximise growth to nearly their physiological maximum, suffer lower mortality rates than in the wild and are usually less prone to infectious diseases [10].

The domestication process tends to produce a coherent set of behavioural, morphological and physiological changes that are similar in many species. A typical domesticated phenotype of a species could therefore be summarised as differing from its wild ancestor in having a different colour (probably being brighter or spotted); being brachycephalic, chondrodystrophic and smaller; having a reduced brain size, earlier sexual maturation and increased reproduction; with a faster and more flexible development; and being less fearful, more sociable, and more risk-prone towards predators. This is a recurrent trait complex that suggests that it may represent a general adaptation pattern to captivity and domestication [1, 15]. Throughout this chapter, we will review these changes and if and how they can affect the welfare of farmed fish.

The domestication of farmed fish is therefore not straightforward, as it depends on the definition of domestication, and how literally that definition is applied to each case. To tackle this difficulty, some authors proposed that domestication in fish should be considered as a process, with progressive stages summarised in **Table 1** [8].

Throughout this chapter and for streamlining purposes, we will adopt the nomenclature given by the authors of the papers cited (e.g. domesticated, artificially selected, strain, etc.), regardless of the stage they appear to be in the classification proposed in **Table 1**.

Domestication level	Description	Examples from FishEthoBase (see Section 4 for a description)
1	Acclimatisation to the culture environment	Malabar trevally (*Carangoides malabaricus*)* Yellowback sea bream (*Dentex tumifrons*)* Spotted sea bass (*Dicentrarchus punctatus*)*
2	Part of the life cycle is completed in captivity, but several important bottlenecks still exist in others (e.g. reproduction, larval rearing, etc.)	Wreckfish (*Polyprion americanus*) Yellowtail amberjack (*Seriola lalandi*) Greater amberjack (*Seriola dumerili*)
3	The entire life cycle is closed in captivity, but with wild inputs	Pangasius (*Pangasianodon hypophthalmus*) Southern bluefin tuna (*Thunnus maccoyii*) Burbot (*Lota lota*) Atlantic halibut (*Hipoglossus hipoglosus*) Senegalese sole (*Solea senegaensis*) Turbot (*Scophthalmus maximus*)
4	The entire life cycle is closed in captivity without wild inputs, but no selective breeding programme is used	Atlantic cod (*Gadus morhua*) Cobia (*Rachycentron canadum*) Meagre (*Argyrosomus regius*) African catfish (*Clarias gariepinus*) Russian sturgeon (*Acipenser guelden-staedtii*) Adriatic sturgeon (*Acipenser naccarii*)
5	Selective breeding programme is used focusing on specific goals (growth rate, fillet yield, flesh quality, etc.)	Common carp (*Cyprinus carpio*) Nile Tilapia (*Oreochromis niloticus*) Gilthead seabream (*Sparus aurata*) European seabass (*Dicentrachus labrax*) Atlantic salmon (*Salmo salar*) Rainbow trout (*Oncorhynchus mykiss*) Siberian sturgeon (*Acipenser baerii*)

*Soon in FishEthoBase.

Table 1. Levels of fish domestication. Adapted from [8].

1.2. Welfare

Definitions of welfare generally vary between the function-based and the feelings-based approaches [16]. Function-based approaches look more into the biological, physiological and overall health perspective of the animal [17]. Feelings-based approaches, on the other hand, link welfare with the emotional (or emotional-like) state of the animal [18] and define welfare in a longer term as the balance between positive and negative subjective experiences [19]. While the first approach might may be too narrow (e.g. a man in prison may be in perfect health and still be experiencing terrible welfare) and the second too wide (how to measure it?),

a behavioural approach may solve the question of incorporating both physiological and mental indicators. Even more, it operationalizes the concept and allows objective measures of welfare [16]. In that sense, we may define welfare as the state of the individual as it copes with the environment [20]. This definition of welfare has several implications: (i) welfare is a characteristic of an animal, not something that is given to it; (ii) welfare will vary from very bad to very good, i.e. along a welfare continuum; (iii) welfare can be measured independently of ethical considerations; (iv) measures of failure and difficulty to cope with the environment give information about how poor the welfare is; (v) knowledge on the biology and life-history of an animal provide essential information about suitable rearing conditions, but direct measurements of the state of the animal must also be used to assess its welfare; and (vi) coping mechanisms may vary among different species, and there are several consequences of failure to cope. Therefore, any one of a variety of measures can indicate that welfare is bad, and the fact that one measure, such as growth, is normal does not mean that welfare is good [21].

2. Natural and artificial selection

In order to understand the effects of artificial selection on welfare-related traits, we must first address natural selection. Although selection acts on differences in survival and reproductive success between individual organisms, or phenotypes, what changes during evolution is the relative frequency of genes. Therefore, Darwin's theory in modern terms may be stated as follows:

1. All organisms have genes coding for proteins and regulating the development of everything in the organism, including the nervous system, muscles and structure of the individual—and so influence its behaviour.
2. Within a population, most genes are present in two or more forms, or alleles, which code for slightly different forms of the same protein or determine when, where and how much of the protein is expressed. These will cause differences in development and function, and so there will be variation within a population.
3. Any allele that results in more surviving copies of itself than its alternative will eventually replace the alternative form in the population. Natural selection is the differential survival of alternative alleles through their effects on replication success.

The individual can be regarded as a temporary vehicle or survival machine by which genes survive and replicate [22]. Because selection of genes is mediated through phenotypes, the most successful genes will usually be those that are most effective in enhancing an individual's survival and reproductive success [23].

The actual basis of selection processes is variation, which is widespread in all biological phenomena. Variations within species are called polymorphisms, and these are (at least partly) independent of ontogeny and sex. This variation is genetically based and heritable [24]. Conversely, phenotypic plasticity can be broadly defined as (i) the ability of one genotype to

produce more than one phenotype when exposed to different environments, (ii) the modification of developmental events by the environment or (iii) the ability of an individual organism to alter its phenotype in response to changes in environmental conditions [25]. Domesticated strains (lineages or populations that have been under artificial selection for generations and that, at least empirically, seem to differ from its wild origin) rely on natural polymorphisms to be selected: for example, present-day domesticated goats are the product of 10,000 years of artificial selection on breeders for specific traits in meat, milk and fur, as well as of natural selection for fitness under variable conditions [3]; fast growing Atlantic salmon (*Salmo salar*) is the result of 40 years of research and artificial selection for fast growing progeny, with an increase of 10–15% in each generation [26].

Although the gap between the time domestication has been underway in terrestrial farm animals and in farmed fish is enormous, there has been a considerable effort towards fish domestication in recent times [4]. However, the main component in the domestication process is the generation interval (i.e. the average age of the parent animals at the birth of their offspring—note that this is *not* the age at maturity). A comparison between land animals and fish may be found in **Figure 1**.

While pig (*Sus scrofa domesticus*), sheep (*Ovis aries*), goat and horse (*Equus ferus caballus*) vary between 1.5 and 3.5 years [27], in fish we may find generation intervals from 6 to 8 months in tilapia [28], 3–4 years in salmon and trout [26], 4–6 years in sea bass and sea bream [29, 30] and eventually from 12 to 33 years in some species of sturgeon [31]. This means that generation intervals may be in the same order of magnitude in terrestrial animals and fish, but also shows how variable these can be for different species in aquaculture. The variation in the average age at reproduction poses a challenge for the establishment of general standards of welfare in fish farming: for example, designing a welfare plan for a tilapia farm will differ immensely from a sturgeon facility.

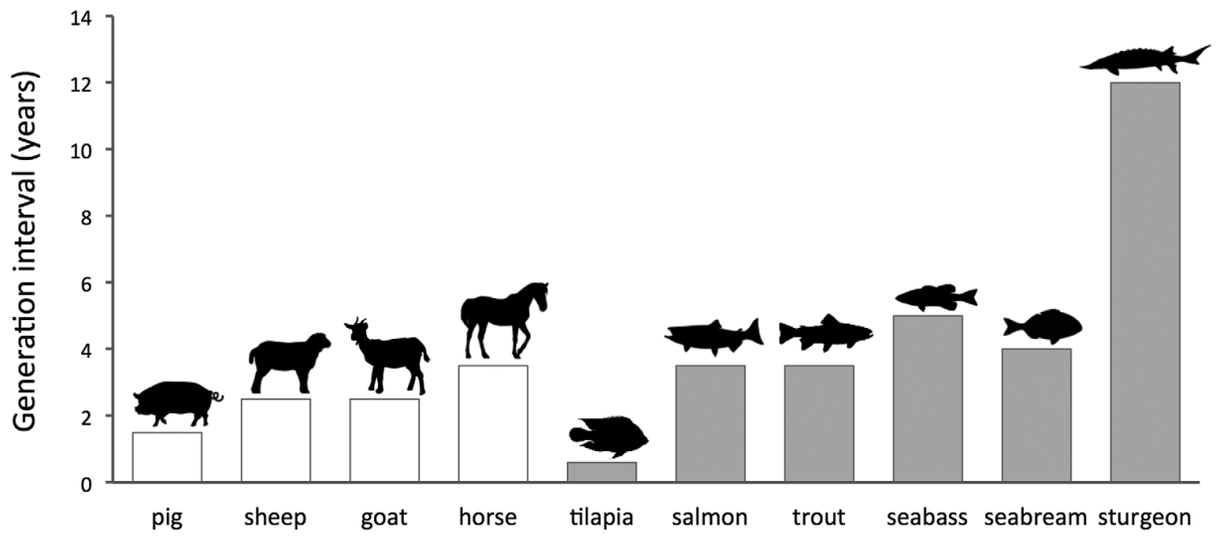

Figure 1. Comparison between the generation intervals in terrestrial farm animals (white bars) and fishes (grey bars).

3. Domestication and welfare

3.1. Genes

In the artificial conditions provided by human farming activities, it is likely that the most successful phenotypes of farmed animals are different from those under natural conditions. However, that does not mean that these selected phenotypes carry differential genotypes, especially due to phenotypic plasticity which is remarkably relevant in fish: different populations of the same species present contrasting yet plastic behavioural responses to environmental and social conditions [32–38]. Nevertheless, artificial selection experiments demonstrate that almost any quantitative trait could be permanently altered, that responses (mostly) occurred as a consequence of changes in the frequencies of genes affecting the traits, and not from mutations, and that many genes must be involved [39, 40].

In livestock species, genetic selection has greatly increased production levels. Usually, the breeding goal is to create a population with high economic production efficiency, i.e. high production combined with relatively low feed intake. Breeding programs have become quite successful because of the high accuracy of breeding value estimation, the moderate to high heritabilities of most production traits and the use of large and fast databases containing production records of many animals and their genetic relationships. Apart from genetic changes, production is also increased by improvement of housing, feed composition, feeding strategies, health status and farm management.

However, negative side-effects of domestication largely occur and are expected to increase when the focus continues to be only on production efficiency. Animals in a population that has been genetically selected for high production efficiency seem to be more at risk for behavioural, physiological, immunological, reproductive and consequently welfare problems [41]. This occurs because behavioural traits, as well as the other typical components of the domestication phenotype (growth, stress, immune function, etc.), are most likely controlled by many genes, i.e. they are polygenic [15]. In addition, a given set of genes may influence different traits, a mechanism known as pleiotropy [42]. In such a case, increasing the frequency of alleles that, for example, up-regulate growth, may at the same time modify other essential welfare-related traits under the influence of the same genes. Finally, the function of one gene may also be influenced by the interaction with other genes, which is known as epistasis [43]. Selection for one or a few traits controlled by genes that have epistatic effects may thus influence a group of other genes, regulating other characters than those selected for. Therefore, both mechanisms (pleiotropy and epistasis) are more than likely to create side-effects on traits that are not desirable [15]. In fact, when animals are selected for production traits mainly, many side-effects have been extensively documented in several species [41]. Some of these side-effects will even affect production itself, such as reduced fertility in fast- growing broilers [41], and are likely to be the target of counter-selection. In other cases, the side-effects may be related to less-obvious traits which may nevertheless have a strong welfare aspect [44] because they shift welfare optima towards unknown directions. These processes have occurred in land animals throughout their domestication. However, the slow and long domestication process on land has allowed both humans and many livestock species to adapt and cope with such

effects. Conversely, the low number of generations in the rapidly increasing, diverse and generally very recent fish farming activity may be too short to permit this adaption in aquatic species.

3.2. Physiology

Changes in the phenotypes of selected farmed fish usually correlate with changes in physiological indicators. For example, when comparing seventh-generation farmed Atlantic salmon with wild individuals, the domesticated fish grow much faster (even more so in salt water where the difference is threefold), pituitary and plasma growth hormone levels were positively correlated with growth rate and significantly higher in the domesticated strain [45]. The same occurs with strains of Brook trout (*Salvelinus fontinalis*) farmed for 30 or more years (ca. 10 generations). The domesticated phenotype is less resilient than the wild, since hatchery-born fingerlings struggle to survive when released into native streams. Moreover, domesticated strains grow better in aquaculture but not in the wild [46], which led some authors to claim that domesticated animals are better adapted to captivity, reducing stress and mortality, increase disease resistance, reduce the use of chemotherapeutics and contribute to better animal welfare and environmental management. Up to 65% of farmed salmon in Norway comes from improved breeding plans, after an extensive programme lasting over 40 years and an enormous investment effort, with numbers reaching nine digits [26]. However, and despite these efforts and claims, 40 years represent only 10–13 generations of farmed salmon (**Figure 1**). Even more importantly, a recent analysis of welfare conditions of farmed salmon revealed a need for improvement in space, substrate, aggression, stress levels and malformations ([47], see *Salmo salar*). A possible conclusion is that the improvement programme of salmon in Norway may be focusing mostly on production-related traits. Although there are improvements on the health perspective of welfare, the natural needs and behaviour of this species in captivity may be generally impaired.

For many physiological indicators such as those listed below, selected strains of farmed fish fail to show positive results:

Metabolic rate: fast growing hatchery strains of Rainbow trout present higher standard metabolic rate (SMR), lower aerobic scope, and potentially lower maximum metabolic rates, suggesting that high growth trades off against a reduced capacity to do metabolic work. Higher SMR of fast growers appears to be related to a greater investment in high-maintenance digestive tissue that supports rapid growth, which appears to compromise active metabolism [48]. Farmed Senegalese sole (*Solea senegalensis*) born from wild spawners are nevertheless capable of shifting their routine metabolism from naturally nocturnal to diurnal, responding to daylight feeding regimes [49].

Hypoxia resistance: triploid strains of domesticated Rainbow trout show faster growth than wild diploid individuals probably due to impaired gametogenesis of 3n fish [50]. Adding to these reproductive problems, triploids are also less resistant to hypoxia [51], which can account for lesser resistance and higher mortalities both in nature [52, 53] and in several types of farming conditions and methods [54–57].

Stress: there are reports of selected strains of farmed fish showing lower stress responses to acute artificial stressors. In Rainbow trout, the cortisol responses to confinement in a net or to electroshock are higher in wild fish than in hatchery-reared animals [58]. However, there are also examples of the opposite pattern, even in the same species: wild trout show lower physiological stress responses to hooking than domesticated trout [59]. Immediate cortisol response to an acute handling stressor in a domesticated Eurasian strain of common carp is also higher than wild Japanese strain [60]. Although cortisol is a universally used indicator for stress, it should be used with caution. This hormone has an adaptive physiological role and several factors (e.g. genetic, developmental, environmental, frequency of exposure) underlie its release upon stressful episodes [61]. An appreciation of these factors, along with knowledge of the biology of the species, solid behavioural observations [16] and secondary stress indicators, such as plasma glucose and lactate [61], are essential for proper interpretation of the data and design of mitigation measures.

Overall performance: wild and hybrid (domesticated × wild) strains of Brook trout showed better rates of recovery (from angling) and yield than a domestic strain [62]; wild strains of Nile tilapia (*Oreochromis niloticus*) perform as well as domesticated strains [63, 64]. Triploid strains of trout also generally tend to have higher malformation rates than wild populations [65].

From the available data on these indicators, it is not clear whether the current domestication process brings any obvious and effective physiological welfare benefits.

3.3. Behaviour

As occurs with terrestrial farm animals, the environment experienced by cultured fishes highly differs from the wild [14, 66, 67]: the physical environment is much simpler, space is restricted, and migration is not possible; food is readily available so long distance tracking of food is unnecessary; there are generally fewer or no predators (apart from human), and they are treated for some diseases. For parent animals, reproduction occurs without the need to compete for mates as it is often the case in the wild. In these aspects, the environment is overall less challenging. In others, however, it is more challenging: fishes are frequently disturbed by human activity, they are usually confined at unnatural densities, which potentially increases the risk of infection and the incidence of social encounters, including aggressive ones, especially when competing for food. The hatchery environment is so different from that experienced in nature that it can potentially generate behavioural differences in three, interlinked ways: (1) differential experience, (2) differential mortality and survival of behavioural phenotypes within a single generation and (3) selection for inherited behavioural traits over several generations [68]. In fact, usual conditions in intensive husbandry favour risk-taking/aggressive fish, as available data suggests that competition for food is major driver for high-risk/high-aggression phenotypes [69]. Hatchery-reared fish are more prone to show higher risk-taking behaviour, which is directly linked with a higher risk of escapes from rearing systems (as in the case of sea cages) [70], and may severely decrease their chances of survival in the wild. Consequently, this leads to a wide range of welfare, environmental and economic consequences. Domesticated strains of guppies (*Poecilia reticulata*), which are not farmed for food but are nevertheless the object of strong artificial selection for aquarium hobbyists, tend to have smaller brains and less cognitive abilities.

This may not only be due to a trade-off between brain size and reproduction [71], but also to the lack of environmental challenges and corresponding cognitive selection pressures.

Despite the consistency of the farming environment, different coping styles (e.g. consistent trait associations such as proactive, active coping or bold, and reactive, passive coping or shy) do emerge in farmed fish [72]. The proactive/reactive continuum has been identified in most farmed species and it should be a factor to consider when designing and evaluating production systems. However, the aquaculture industry selects mostly for growth performance [73] and proactive fish grow faster [74]. Consequently, there is a theoretical infinite selection for proactive and aggressive individuals in fish farming. This creates an obvious welfare problem that can only be solved by a deep understanding of the biology of the species as well as through the design of appropriate and diverse farming environments, which can accommodate different coping styles, even at the expense of lower production outputs [72]. In addition to coping styles, there is another source of intrinsic variability in animals that is phenotypic plasticity, best explained by behavioural reaction norms (BRN, i.e. the set of behavioural phenotypes that a single individual produces in a given set of environments) [75]. The BRN may actually be calculated, and it incorporates information on how an animal behaves on average and how its behaviour changes over a gradient, specifying the precise form of the relationship between response value and environmental condition. The relationships between food provisioning rate and begging intensity, between dispersal behaviour and current velocity, or between anti-predator behaviour and predation risk are all examples of BRNs. This approach treats both inter-individual and intra-individual variance in behaviour as meaningful (rather than as 'noise') [76].

The implications of the domestication process on the behavioural perspective of welfare are therefore far from simple. Behavioural changes due to generations in captivity do seem to occur but (1) they are accompanied by physiological and cognitive modifications that are challenging to accommodate in good welfare, and (2) while the behavioural phenotypes of wild fish are adaptive and selected throughout stable evolutionary pressures, captive phenotypes are responding to extremely different settings that are artificially rapid and that can often push welfare needs into collision with traits required for production.

The available evidence, however, is largely based on data from salmonids. These species are nonetheless far from representing the majority of production of finfish in global aquaculture: Atlantic salmon ranks seventh in production worldwide with approximately 2.4 million tonnes in 2015 (less than half of the production of the #1, Grass carp (*Ctenopharyngodon idella*) with 5.8 million tonnes) [77].

3.4. Sensory worlds

Fish are an extraordinary group of animals. Our 'underwater cousins', as Jonathan Balcombe describes them in his book *What a fish knows* [78], are the closest living relatives to our common aquatic ancestor. But, as with most distant family members, our understanding of their lives is limited. Even though ichthyology was incorporated as a formal science by Aristotle (383–322BC) [79], we still struggle to understand many aspects of fish biology. Those limitations to our knowledge of fish arise mainly from the fact that fish live in water. This posts a strong barrier

for the direct observation of these animals, and up until recently the study of fish was restricted to investigation from the surface under particular conditions of water transparency and shallow depth, the examination of dead specimen or watching captive animals in artificial conditions. This constraint was only truly overcome with the invention of the self-contained underwater breathing apparatus by Jacques-Yves Cousteau and Emille Gagnan in 1942. Thus, only roughly 80 years ago could humans consistently observe fish in their natural habitats, in a similar way than we had been doing with terrestrial animals since the dawn of our species. This gap in the knowledge of fish biology is a major drawback for the establishment of welfare standards. Since self-experience and individual knowledge are impossible to be observed directly, their existence in other species tends to be forgotten or ignored, especially in taxa with which we do not readily identify or that are distantly related to us [80]. While we as humans can easily empathise with cattle, goats, sheep, horses and other terrestrial animals because they have been living next to us for millennia and share most of our sensory world, fishes exist in a realm of their own.

In fact, there are likely to be substantial differences in fish sensory systems compared with a terrestrial animal due to differing ecological and evolutionary pressures [81]. The term *Umwelt* was coined by Jakob von Uexküll in 1909 and refers to the sensory world of an animal—i.e. a *subject*—who is perceiving and actively responding to environmental stimuli. Moreover, the animal is not reacting mechanically to the world, and instead building its *Umwelt* with a meaningful living strategy, even though the behaviours may not be consciously planned [82]. This concept is of vital importance for the design of welfare solutions for captive fishes, because the sensory world of these animals differs highly from our own experience, is extraordinarily diverse, and relies on senses that differ from ours.

3.4.1. Vision

Light behaves differently underwater than at the surface and can be influenced by physical and biological factors. Depth can modulate the wavelength (i.e. the colour), while intensity and scatter can be modified by turbidity and suspended particle type. These can also change rapidly with daytime, season or weather conditions. Furthermore, species have different visual systems depending on their life-history (e.g. predators that rely on visual cues for feeding, fishes that are common preys and must remain vigilant for evasion) or even within life stages (e.g. larvae that live in the depths and move to shallower depth when they grow, species with ocean juveniles and freshwater adults). These environmental changes represent huge selective pressures for the radiation of visual systems in fish. Not surprisingly, there is an enormous variety not only in the type of eyes that can be found in fish [83], but also in the brain structures that process visual information [84].

3.4.2. Chemical sensing

Chemical senses serve an essential ecological role and are extremely relevant in communication contexts in all groups of fish (cyclostomes, elasmobranchs and teleosts). They enable orientation in the dark or blurry waters, predation, foraging and escape from predators for example [85]. Chemical sensing also serves intra-specific communication, allowing males and females to find suitable partners [86], as well as competitors to assess and announce their status in agonistic contexts, which are solved much quicker and less violently thanks to 'chemical diplomacy' [87, 88].

Chemical sensing in fish exists in three modalities: olfaction, solitary chemosensory cells and taste. Olfaction may function at a larger distance for all the roles described above, and olfactory receptors are usually located in the nostrils on the most anterior part of the head. Taste cells are usually limited to very close range detection of foodstuffs and are located in the head and mouth [85]. In most predatory fishes, the taste system is used solely during oral food evaluation [89]. Solitary chemosensory cells are not well described yet but may serve as food, predator or conspecific locators, spread throughout the body of the animal [85].

3.4.3. Hearing

In all fishes, sound is detected by one or more of the otolith organs. As sound passes through a fish and brings its tissues into motion, the otoliths respond to sound-induced motions of the animal's body. In many fish species, named hearing specialists, the otoliths may also receive a displacement input from the swimbladder or another gas-filled chamber near the ears. These fishes may respond to both acoustic pressure and particle motion with a particularly efficient coupling between the gas bladder and the otolith organs and tend to have very high sensitivity to sound [80].

In addition, fishes have evolved a diversity of sound-generating organs. These include vibrating the swimbladder and pectoral girdle or rubbing bony elements against each other. Sounds are produced in various behavioural contexts (agonistic interactions, courtship, spawning and in distress). Similarly to chemical communication, acoustic signals may serve in decreasing aggression, assessment of the fighting abilities, species recognition, mate attraction and mate choice [90].

3.4.4. Nociception

The aquatic environment influences basic perception and adaptation to damage in fishes: for example, they cannot fall because of buoyancy in the water column and this prevents injury due to gravity; noxious chemicals entering the aquatic environment may be diluted and thus pose a lower risk; and major shifts in temperature are less common compared with terrestrial environments. This could mean fishes experience less risk of damage than terrestrial animals, and it may be reflected in their nociceptive system [81]. In fact, although receptors for damaging stimuli have been found in all fish groups, and fishes possess neuroanatomical pathways comparable to those found in other vertebrate groups, there are interesting differences that reveal adaptions to evolutionary pressures: for example, rainbow trout nociceptors are not activated in low temperatures, because they live in cold water [91], but they are more sensitive to mechanical stimuli than mammals, probably because their skin is more fragile, and to heat, probably because they live in temperatures usually not above to 25°C [92]. The Chameleon cichlid (*Australoheros facetus*), on the other hand, is far more tolerant to heat exposure, which can also be explained by its broad ecological distribution [93]. Importantly, fish are ectothermic, and therefore their inner temperature depends on the environment (typically 0–30°C). As mammals maintain homeostasis at 37°C, it is likely that fish nociceptors have a lower temperature threshold than mammals [81].

Interestingly, the same groups of substances that reduce pain in humans (opioids, anti-inflammatory drugs and local anaesthetics) are also effective in reducing behavioural and physiological indicators of discomfort in teleosts, which is indicative of similar sensing mechanisms [81].

3.4.5. Other senses

There are sensory systems in fish that are completely alien to us. The lateral line for example, which serves as a receptor for hydrodynamic stimuli such as those generated by conspecifics, predators or prey. Although the biological processing of hydrodynamic signals has been well studied, not much is known about how fish can discern these from natural occurring events [94]. As all fishes experience night, darkness or turbid waters, there is strong selection for the use of non-visual senses in all fish species. Anatomical diversity suggests that the lateral line is one of the most important senses for fishes. However, research on the function of the lateral line has lagged due to poor understanding of hydrodynamics at small scales and lack of this sense in humans, making it difficult to imagine a fish's hydromechanical world [95]. Electrical sensing is ancestral to fishes and is present in most non-teleosts as well as certain teleost species. The electrosensory world of fishes is rich with electric fields from a multitude of sources including the earth's magnetic field and the bodies of all aquatic organisms including the electrosensing fish itself. The fish's extremely high sensitivity to these fields enables orientation, navigation, communication, and even detection and localization of other fish, both prey and conspecifics [96–98]. **Figure 2** summarises the sensory world of fish.

Not only the sensory world of fishes is difficult to relate to, but also the physics of movement underwater in a three-dimensional world can be challenging to understand for humans, who exist roughly in a 2D world. Despite this challenge, it is nonetheless a critical next step for the

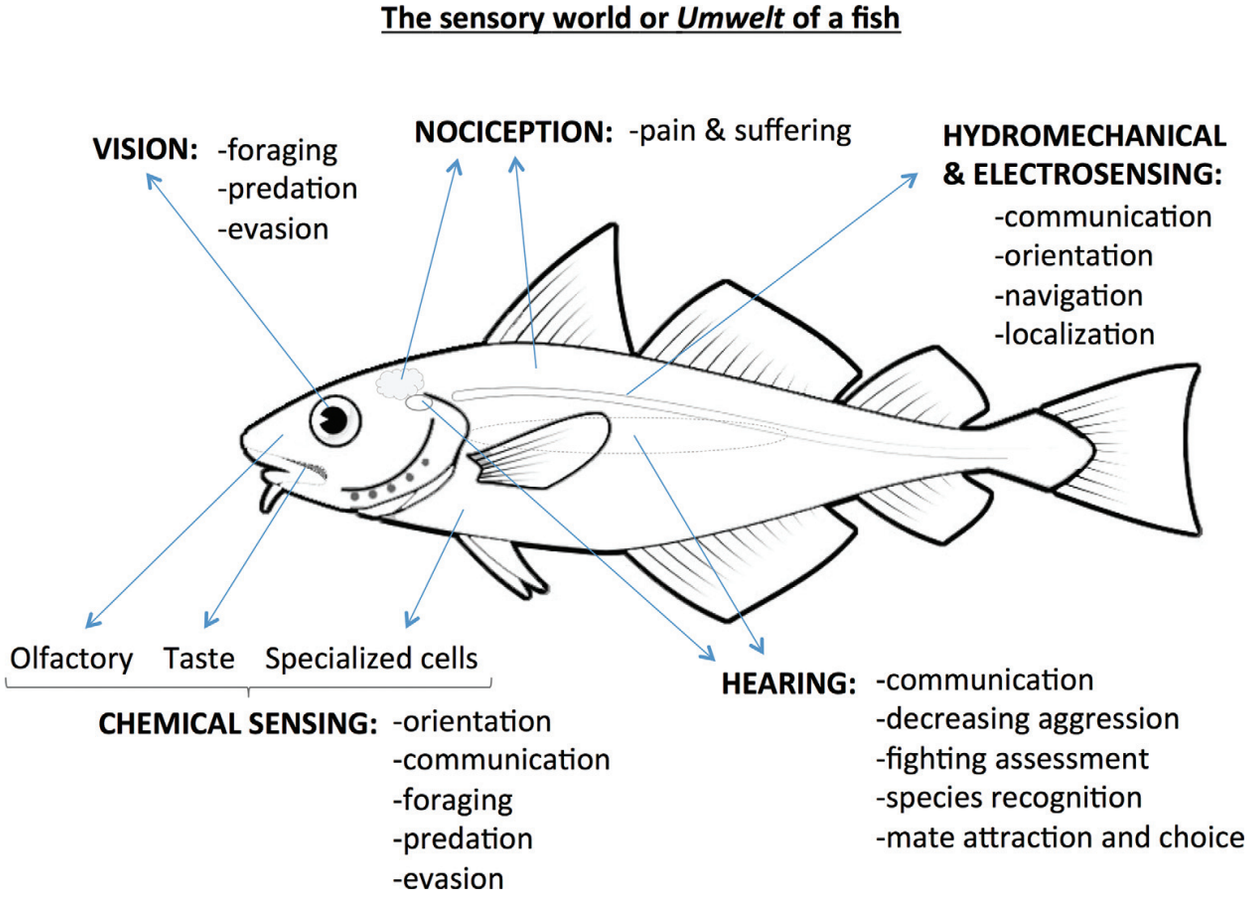

Figure 2. The sensory worlds of fish.

understanding of fish locomotion, and the design of appropriate rearing systems. The 3D nature of fish functional design is clearly demonstrated in the enormous diversity of body shapes and swimming modes in fishes [99].

Other physical properties of water affect fish in a different way than dry land does to farm animals: for example, water is a dense medium, so fish are constrained by hydrodynamic demands and fast swimming can be costly; gases dissolve readily in water, but moving water for oxygen extraction is energetically costly; many other chemicals readily dissolve and disperse in water.

In order to adapt to such a different medium, fishes not only develop the extraordinary sensory systems we have discussed above, but also show many amazing morphological and physiological adaptations, that can strongly determine welfare needs: they may undergo dramatic changes in form and function across life stages, as in the case of flatfishes [100]; unlike mammals but in common with birds, fish red blood cells are nucleated, giving them additional functions including immune responses [68]; fish grow continuously [101], influencing their relation with space and density across time; most species excrete ammonia (which is highly toxic, especially in aquaculture conditions [102]) while land animals excrete urea [103]. Finally, fish have more genes, more gene variability and more gene duplicates than terrestrial animals [104, 105].

To summarise, the extraordinary features of the aquatic environment, the exotic adaptations of fish and their *Umwelt* represent a challenge for the assessment of fish welfare. Only through a deep understanding not only of the fundamental differences between fish and terrestrial farm animals but also of the specific needs of each species can we design appropriate measures to improve and establish high standards of welfare in aquaculture. This task becomes even more daunting considering the number of animal species currently being farmed in aquatic environments: 362 finfishes (including hybrids), 104 molluscs, 62 crustaceans, 6 frogs and reptiles, and 9 aquatic invertebrates [106]. For the sake of comparison, there are 26 well-studied species of terrestrial farm animals, according to the Domestic Animal Diversity Information System (DAD-IS) [107]. Due to their low number of species, welfare measures and standards are easier to establish for land animals than for fishes. With such a long list of fish species in current world farming, how to tackle the issue of assessing fish welfare in a global manner?

4. Assessing welfare in farmed fish

Welfare in aquaculture has been a motive of academic work in the recent past. Several authors have addressed the topic in reviews and research papers [16, 68, 108–110], and the COST action *Welfare of fish in European aquaculture* has been promoted aiming to (i) improve the knowledge on welfare of fish, (ii) formulate a set of guidelines embodying a common and scientifically sound understanding of the concept of welfare in farmed fish, and (iii) construct a range of targeted operational welfare indicator protocols to be used in the industry [111]. The results of this action were incorporated in many research projects, not only in Europe but also in the USA, Canada, and New Zealand. In addition, major stakeholders in the industry were also

involved, including the European Aquaculture Associations, the Fish Farmers Association and the scientific department of EU responsible for fish welfare.

In recent years, the FishEthoBase project (http://fishethobase.net) has been working in order to bridge the gap even further between the scientific community and the fish farming industry. This open-access database on fish ethology and welfare provides a platform where scientific knowledge is scrutinised and summarised in order to answer relevant criteria regarding welfare in aquatic animal farming. The aim is to cover all fishes farmed nowadays as well as other aquatic species, delivering concrete solutions for fish farmers, pointing to knowledge gaps for researchers and providing awareness for the general public and other stakeholders. This is accomplished in two ways: (1) full profiles of farmed species, where over 40 criteria and sub-criteria on ethology, but also ecology, physiology and general biology are reviewed in-depth according to the scientific literature. Based on these findings, a series of recommendations are proposed to address identified welfare issues in aquaculture; (2) short profiles of farmed species, where a sharp evaluation of 10 critical criteria is performed, covering ecological, behavioural and physiological traits transversal to all fish species: home and depth range, migration, reproduction, aggregation, aggression, habitat type, stress, malformations and slaughter. In addition, sustainable feeding and domestication are also addressed. These 10 criteria are answered using a welfare assessment protocol based on standardised risk analysis methods. For each species, this protocol provides (i) a comparison between the wild behaviour and the fish welfare state under conventional farming conditions, (ii) the overall welfare potential and (iii) the certainty of our findings. The sum of high scores of each species in these three measures throughout all 10 criteria results in the FishEthoScore, an index that summarises the general welfare state of the species. As occurs with all indexes, the FishEthoScore incurs the risk of oversimplifying a complex array of data concerning welfare. However, by asking the same questions to (ultimately) all farmed fish species, it offers a unique possibility not only for a comparative approach, but also for a global perspective on which species may be farmed most humanely. This is apparently the first effort to create such a welfare assessment scheme for aquaculture, and it may constitute a decisive step for a near-future welfare certification in the industry.

5. Fish domestication and the Five Freedoms

The concept of the Five Freedoms was coined in 1965 in the Brambell Report [112] concerning husbandry of livestock and revised by the Farm Welfare Council of the UK in 1979 into its present form [113]:

(I) Freedom from hunger and thirst—by ready access to fresh water and a diet to maintain full health and vigour;

(II) Freedom from discomfort—by providing an appropriate environment including shelter and a comfortable resting area;

(III) Freedom from pain, injury or disease—by prevention or rapid diagnosis and treatment;

(IV) Freedom to express normal behaviour—by providing sufficient space, proper facilities and company of the animal's own kind;

(V) Freedom from fear and distress—by ensuring conditions and treatment that avoid mental suffering.

This concept forms the basis of recommendations and legislations worldwide and, despite their age, are extensively employed for academic, educational and veterinary purposes with great practical utility [113]. Also, they paved the way so that animals could be considered by European law as sentient beings in the Lisbon Treaty of 2007 [114].

Research on animal sentience, situated between ethology and psychology, was initiated by ethologists such as Dawkins [115, 116] and cognitive psychologists such as Toates [117], around the early 1980's. These studies allowed a deeper understanding of animal minds and depicted how animals perceive the world and how environmental stimuli may affect their welfare level. Most importantly, they opened the door to the understanding of animal's subjective experiences. These experiences may be positive and negative, and the latter include suffering, which is fundamentally a wide range of unpleasant emotional (or emotion-like) states. Negative experiences occur when unpleasant subjective feelings are acute or continue for a long time when an animal is unable to carry out the actions that would normally reduce risks to life and reproduction in those circumstances [115, 118].

The five freedoms concept is nonetheless criticised. Some authors claim that this framework is overly guided by anthropocentric thinking about how animals ought to be handled, neglects the concept of allostasis (stability through change) and generally reflects a more ethical view than a science-based approach [119]. The concept may be misleading on, for example, stress and stress indicators such as cortisol [120], because it is well known that stress hormones are also involved in healthy adaptation [121–123]. Capacity to change, allostasis and biologically relevant challenges are crucial for good health and welfare, therefore stable conditions and homeostasis should not be considered optimal [119, 124]. As discussed in Section 3, phenotypes that are selected exclusively for production traits often show signs of structural and morphological imbalance. This occurs because symmorphosis (i.e. a match between structural design and functional demand) is disrupted [125]. In many farm animals (e.g. broiler chickens or heavily selected strains of trout), the structural design of internal organs does not match functional demand [48, 126]. This imbalance is responsible for many health problems in farm animals.

The Concept of Animal Welfare based on Allostasis aims to be an alternative to the Five Freedoms. It incorporates recent scientific developments in behavioural physiology and neurobiology and can be summarised as follows [119]:

- Stability through change (allostasis) and capacity to change are crucial to good health and good animal welfare. Health in this concept has the same meaning as defined in the World Health Organisation's (WHO) constitution as 'a state of complete physical, mental and social well-being and not merely the absence of disease or infirmity' [127].

- Good animal welfare is characterised by a broad predictive physiological and behavioural capacity to anticipate environmental challenges.
- Good animal welfare is guaranteed when the regulatory range of allostatic mechanisms matches the environmental demands.
- A low allostatic load (not very low or zero) is key for good health and good animal welfare.
- Symmorphosis should be respected.
- Behaviour and physiology should be interpreted in terms of animal perceptions and not exclusively in terms of human values.

To summarise, the Five Freedoms were primarily derived in relation to the welfare of farm animals, but, with the exception of the fifth freedom, would appear to consider that animals are passive within their environment [128]. Despite its undeniable role in the development of present (and future) welfare standards, this concept would benefit from an update in order to incorporate both ultimate (i.e. adaptive) and proximate (i.e. physiological) mechanisms. Integrating phylogeny and ontogeny in the design and analysis of husbandry practices would result in broader and overall better welfare schemes (**Figure 3**).

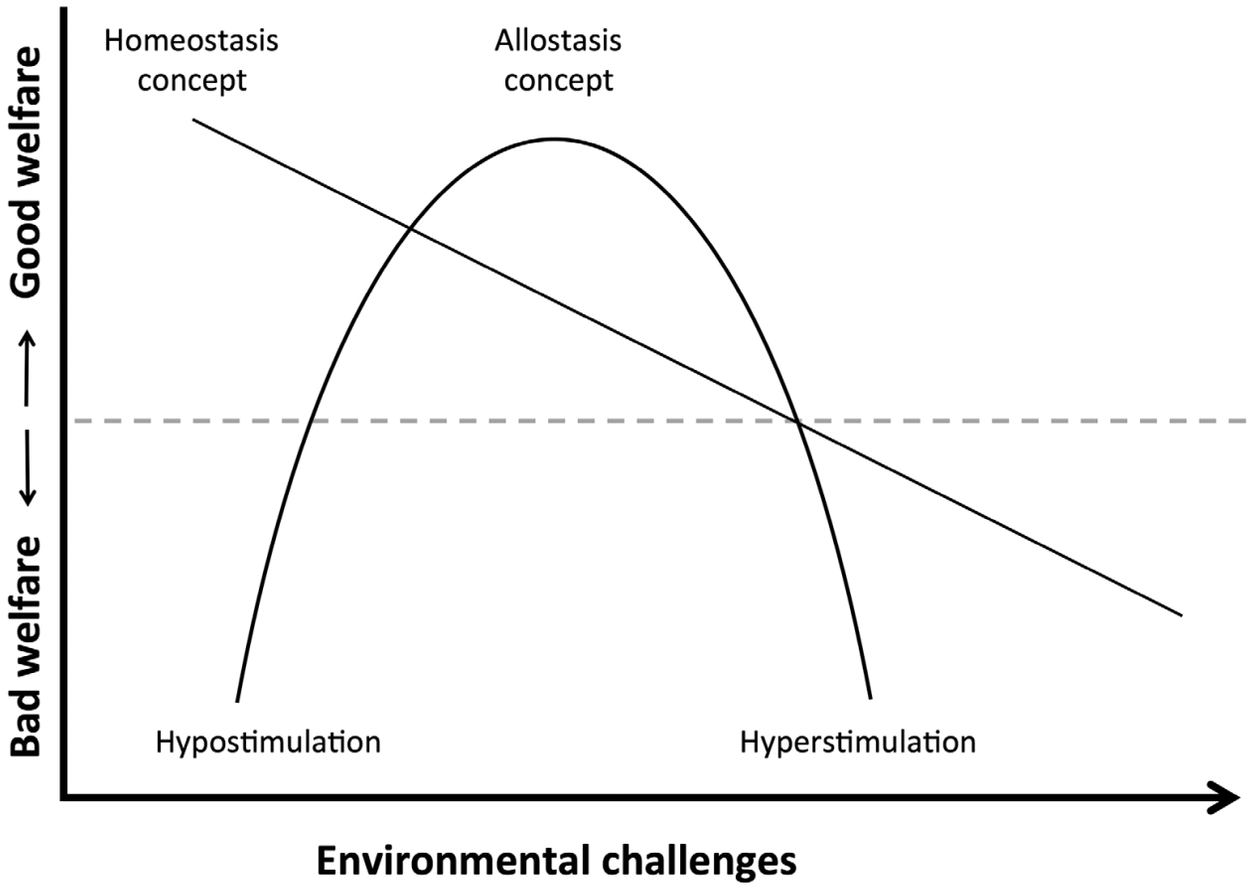

Figure 3. Animal welfare in relation to environmental challenges as shown by the out-dated concept based on homeostasis and the new concept based on allostasis. Adapted from [117].

6. Ethics vs. welfare in fish domestication

The ethical discussion on welfare of animals is controversial. This occurs because often the perspectives of scientists studying welfare science(s) and philosophers debating about ethics lie on very different standpoints. While science uses mostly operational and measurable concepts, such as the ones described throughout this chapter, ethics is focused on experiencing values and critically reflecting on them. Three main ethical theories are followed:

- The contract theory states that, despite the naturally selfish nature of man, there is a need to waiver rights in exchange for the benefits of a contract (implicit or explicit) [129];
- The utilitarianism theory states that the best action is the one that maximises utility, and therefore actions are to be evaluated majorly for their consequences [129];
- The deontologist theory states that the ethical value of an action is dependent on the motivation behind it and not on the consequences. It criticises the utilitarianism theory stating that the right of the individual can never be sacrificed for the common good [130].

The following allegory provides a good metaphor for the misunderstanding between philosophers and scientists:

'Two dog owners met one day to walk their dogs together. One owner had grown up in a small family that valued health, safety, and orderly, disciplined behaviour. The dog of this owner received regular veterinary care, two meals a day of low-fat dog food, and was walked on a leash. The other owner had grown up in a large community that valued conviviality, sharing of resources and close contact with the natural world. This dog (the owner's third - the first two had been killed by cars) had burrs in its coat, was fed generously but sporadically, and had never worn a collar in its life. Each owner, judging quality of life from very different viewpoints, felt sorry for the other's dog' [131].

The challenge lies in the different concepts, assumptions and vocabulary that scientists and philosophers use, which function as two distinct cultures with little mutual understanding or communication. Since the early days of the animal welfare debate, the two sides have struggled to communicate with each other, even though both were (and are) working with the common goal of understanding and improving an appropriate relationship between humans and other species of animals [132]. In fact, scientific research on animal welfare began because of ethical concerns over the quality of life of animals, and the public looks to animal welfare research for guidance regarding these concerns. The conception of animal welfare used by scientists must therefore relate to these ethical concerns in order to make sure that the orientation of the research and the interpretation of the findings are to address them successfully [131]. In order to bridge the gap and seek common ground between ethics and welfare science, it is important to recognise three classes of problems that may arise when the adaptations present in an animal do not fully correspond to the challenges posed by its current environment. These problems summarise the ethical concerns about the quality of life of animals [131]:

- If animals present adaptations that no longer serve a significant function in the new environment, then unpleasant subjective experiences may arise, yet these may not be

accompanied by significant disruption of biological functioning. For example, species such as sea bream farmed in an open water sea cage may experience a strong, not full-filled need to seek shelter or forage on the sea bottom;

- If the environment poses challenges for which the animal has no corresponding adaptation, then functional problems may arise, even if not accompanied by significant effects on emotional-like states. Thus, a fish being fed with feed with incorrect lipid content will accumulate unhealthy body fat without appearing to notice or mind the problem;
- Where animals have adaptations corresponding to the kinds of environmental challenges they face, problems may still arise if the adaptations prove inadequate. For example, tilapia farmed in too cold water or trout farmed in too warm water will not be able to adequately regulate temperature, leading to functional failure as well as to a negative mental experience.

Animal welfare science has grown more compatible with the approaches used by some ethicists. Some scientists have recognised the interplay of normative and empirical elements in the assessment of animal welfare, and many are attempting to understand ethically relevant subjective experiences of animals. This convergence of the scientific and philosophical approaches may lead to a more integrated field of study and to a greater awareness that neither empirical information nor ethical reflection can, by themselves, answer questions about our proper relationship with animals of other species [132].

7. Conclusions

Considering that the domestication process in fishes is still in its early stages, determining whether and how this process affects welfare is not a straightforward task. Our understanding of fish biology is millennia behind that of terrestrial mammals, and the life-history of fish can be highly complex, with many species presenting stages that completely differ in every aspect from the final adult form. Furthermore, the sensory worlds of fish are very different from our own, and only recently have we begun to scratch the surface of the minds of fish, which hinders the establishment of empathy with our underwater relatives. To complicate things even more, fish farming is not focused on a few species, as in the case of land animals, but rather on hundreds of species that the industry invested in rearing for human consumption. Finally, the key concepts guiding welfare in farm animals are currently out-dated and seem to be insufficient to tackle a complex and diverse animal group such as fishes. The present review shows that domestication is not necessarily related to better welfare of fish especially because the traits the industry is selecting throughout the domestication process are generally focused on production (e.g. faster growth, larger mass), without taking into consideration pleiotropic or epistatic effects on other systems and on the organism. This knowledge gap should be bridged with research, either through species-specific approaches such as the COST action *Welfare of fish in European aquaculture* or broader frameworks such as FishEthoBase. Only by integrating the research and the industry, and by finding common

grounds between ethics and science, can we expect to build species-appropriate and ethically justifiable systems in which to farm aquatic species.

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